Ovipositional Response of Indianmeal Moth (Lepidoptera: Pyralidae) to Size, Quality, and Number of Food Patches

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ABSTRACT Indianmeal moth, *Plodia interpunctella* (Hübner), is one of the most important pests in retail stores and processed food facilities, but little is known about its ovipositional response to varying sizes and qualities of food sources. In this study, we monitored oviposition for 48 hours divided into 16 consecutive 3-h intervals, and found that, on average, *P. interpunctella* females laid eggs 6.4 times. We found a positive correlation between number of oviposition events and total oviposition. We conducted laboratory experiments to examine the distribution of eggs laid by *P. interpunctella* females in dishes that varied in size and number. Experiments were conducted with "improved" food (cracked or walnut oil-treated wheat kernels) and "control" food (plain untreated wheat kernels). In trials with dishes of two different sizes, *P. interpunctella* females seemed to distribute eggs according to the surface area of dishes regardless of the food. In trials with improved food, total oviposition was positively associated with the number of dishes, whereas the number of control dishes had no apparent effect on total oviposition. In trials with one improved food dish and one to eight control food dishes, *P. interpunctella* females consistently preferred oil-treated wheat kernels, whereas they showed no preference for cracked wheat kernels. Using an index of randomness (D_p), we demonstrated that the distribution of eggs was significantly different from a Poisson distribution, thus indicating that it was nonrandom, regardless of the number of dishes. Using an index of aggregation (I_{m2}), we showed that for all the foods, the distribution of eggs became increasingly aggregated with higher numbers of dishes and that this trend was most pronounced in trials with improved foods.

KEY WORDS behavior, egg distribution, ovipositional strategy, stored-products

IN STUDIES OF OPTIMAL foraging strategies in insects, the main objective is to increase the knowledge about mechanisms that are responsible for nonrandom foraging within a given sampling space (Hassell and Southwood 1978). However, the concept of optimal foraging concerns not only the foraging behavior of insect individuals for resources that provide immediate reward in the form of food or energy. The same mechanisms are involved in selection of suitable sites by ovipositing females, because those mechanisms determine food availability for the offspring. In a sampling space with multiple food patches available, an ovipositing female insect may generally follow one of three expected strategies in distributing eggs among available food patches: 1) randomly, 2) evenly, or 3) most of the eggs in few food patches (clumped). The first distribution pattern would be expected if females possess limited control over how many eggs are laid in a given oviposition event and are unable to assess the quality of food patches. The second distribution pattern would be expected if females control how many eggs are laid in a given oviposition event but are unable to assess the quality of food patches. The third distribution pattern would be expected if females control how many eggs are laid in a given oviposition event and are able to assess the quality of food patches. The latter distribution of eggs would suggest that an optimal distribution strategy may be in place (e.g., ideal free distribution; Fretwell and Lucas 1970).

Stored-product environments provide a heterogeneous variety of microhabitats, some of which can serve as oviposition sites (Roesli et al. 2003). The management practices in food facilities often imply frequent disturbance of potential food patches, due to sanitation, stock rotation, and/or food production. Given the variety of food items and high level of human disturbance, a fundamental question is: How do economically important insect pests adapt to such unstable and heterogeneous environments? Despite the importance of understanding how the foraging/ovipositional strategy of stored-product insect populations under field conditions is affected by food availability and food quality, we are unaware of research studies addressing this issue. Several studies have examined ovipositional response by stored-product insects to number and quality of food sources under laboratory conditions (Campbell 2002, Campbell and

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Runnion 2003, Nansen and Phillips 2003), and such studies can potentially provide initial insight into the ovipositional strategies of insect pest populations under real-world conditions.

Plodia interpunctella (Hübner) is considered the most important stored-product pest in many U.S. states (Mueller 1998, Platt et al. 1998) and causes economic losses on both raw and processed food commodities (Lecato 1976, Storey et al. 1983, Cline and Highland 1985, Cox and Bell 1991, Bowditch and Madden 1996, Johnson et al. 2002, Nansen et al. 2003a). Monitoring and sampling programs for this important insect pest are based almost exclusively on interpretation of pheromone trap captures of moth males (Phillips et al. 2000). Despite the considerable reliance on interpretation of pheromone trap captures in applied moth control, there are, to our knowledge, no exhaustive studies of the relationship between pheromone-baited trap captures of moth males and the spatial distribution of adults or larval stages, which are responsible for the economic damage. Nansen et al. (2004) analyzed the spatial distribution of *P. interpunctella* adults and larvae and showed that the distribution of larvae in the grain was aggregated, whereas that of adults captured at two heights above the grain was random. An aggregated distribution of feeding larvae and a random distribution of nonfeeding adults in a habitat where food is apparently everywhere and not limiting suggests that females may direct oviposition according to conditions other than simply the presence or absence of food. Monitoring devices for *P. interpunctella* females are therefore needed to improve our understanding of their movement patterns and ovipositional strategy.

In this study, we conducted laboratory experiments to determine to what extent the distribution of eggs laid by *P. interpunctella* females was affected by the size, quality, and number of food patches. This study is part of an on-going research effort toward the description of female reproductive and host-finding behavior in *P. interpunctella.*

Materials and Methods

Insects and Experiments. *P. interpunctella* adults from the laboratory culture at Oklahoma State University were reared at a photoperiod of 16:8 (L:D) h, 28°C, and 60–70% RH on a standard diet (Phillips and Strand 1994). The laboratory colony originated from moths collected in Stillwater, OK, in 1997, and infusions of wild moths from the same location are made to the colony yearly. Recent comparisons between wild and laboratory moths revealed no behavioral differences with respect to oviposition responses to key oviposition stimulants (T.W.P., unpublished data). Pupae were sexed and carefully transferred to individual vials where they were kept until 1 to 2 d after emergence to ensure that only young naive virgins were used in the experiments. One female and one male were used in each experiment, and *P. interpunctella* individuals were used only once. Experiments were conducted in transparent plastic boxes that measured 17 by 31 by 8 cm (width by length by height). The floor inside test boxes was covered with brown craft paper, which was replaced after each trial. The number of eggs laid per female was used to quantify how *P. interpunctella* females assessed the value of food patches. In all trials, numbers of eggs were determined inside the dishes and on the box floor. "Total oviposition" denotes the total number of eggs laid by a single *P. interpunctella* female during 48 h in each trial. Results from boxes were included only if both adults were alive after 48 h and total oviposition >20 eggs. For each combination of dishes, 5–10 replicated trials were conducted on at least two separate dates, so that 15–20 replications were conducted for each experiment.

Resource Value of Dishes. As in Nansen and Phillips (2003), we use the term "dish" to refer to a 5- or 10-cm-diameter petri dish containing wheat kernels. The term "resource value" is used to describe the difference between types of dishes, and experiments were conducted to evaluate the ovipositional response to dishes with varying quantity and quality of food. Three different foods were used: 1) untreated whole wheat kernels (control); 2) cracked wheat (cracked), which consisted of ground whole wheat kernels that had been passed through U.S. sieve #8 and retained by U.S. sieve #14 (particle size 1.40–2.36 mm); and 3) whole wheat kernels treated with cold-pressed walnut oil (Loriva) at a dosage of 0.5 μl/g wheat (oil-treated). Oil-treated wheat and cracked wheat were used to evaluate the effect of providing foods with either different nutritional (oil-treated) or physical (cracked) qualities. Nansen and Phillips (2003) demonstrated that *P. interpunctella* females preferred to oviposit on wheat kernels treated with walnut oil compared with wheat kernels treated with oils of other species of seeds and nuts and compared with untreated wheat kernels. According to Nansen et al. (2003b), the dosage of walnut oil added to whole wheat kernels in this experiment was considered within a range that elicits positive ovipositional response by *P. interpunctella* females. We used cracked wheat, because it has the same nutritional value as whole wheat but has a different physical structure, and *P. interpunctella* have lower mortality on cracked versus whole wheat kernels (Lecato 1976). The term "improved dish" denotes a single dish containing either cracked wheat or oil-treated wheat when offered simultaneously with "control dishes" (containing untreated wheat kernels).

Number of Oviposition Events. The purpose of this experiment was to determine the number of oviposition events during 48 consecutive hours divided into 3-h intervals. Ten pairs (one male and one female) of *P. interpunctella* adults were placed separately in 150-ml glass jars containing 50 ml of whole untreated wheat kernels. Every three hours for 48 h, each pair of moths was transferred to a new glass jar with wheat kernels, and the number of eggs laid was determined. This experiment was conducted under ambient light conditions at 20°C.

Ovipositional Response to Size of Dishes. The purpose of this experiment was to evaluate whether ovipositing *P. interpunctella* females responded to dishes of different sizes. In a three-choice experiment, two 5-cm-diameter dishes each with 10 g of food were offered simultaneously with one 10-cm-diameter dish containing 20 g of food. An additional objective in this experiment was to determine whether the number of eggs laid in the large dish was affected by the total oviposition. If ovipositing *P. interpunctella* females lay eggs mainly as a function of "point" sources of food and without regard to quantity of food per dish, one would expect the average number of eggs per dish to be about the same irrespective of dish size (33% of total oviposition in the large dish). The surface area of a small dish equals 19.6 cm^2, and the surface area of a large dish equals 78.6 cm^2. Thus, if the eggs are distributed according to the surface area of dishes one would expect 4 times as many eggs in the large dish compared with the number of eggs laid in one of the small dishes (equal to 66% of total oviposition in the large dish). If moths laid eggs depending on the amount (mass or volume) of food in dishes, one would expect half of the eggs laid in the large dish (20 g of wheat kernels) and a quarter of the eggs laid in each of the small dishes (10 g of wheat kernels in each). Twenty replications were conducted for each food, and we compared observed and predicted numbers of eggs in the large dish for the three distributions of eggs.

Ovipositional Response to Resource Value of Dishes. The purpose of this experiment was to determine whether *P. interpunctella* females prefer to oviposit in one 5-cm improved dish when offered simultaneously with 1-, 2-, 4-, or 8 5-cm control dishes. We used a χ^2 test to compare the proportion of eggs in the improved dish with what would be expected from random oviposition among all dishes (no preference). For instance, in trials with one improved dish and four control dishes, no preference for the improved dish would be if the number of eggs laid was not significantly different from 20% of the total number of eggs laid in all five dishes.

Ovipositional Response to Number of Dishes. The purpose of this experiment was to determine how the total number of eggs laid and the distribution of eggs among dishes were affected by the number and quality of available dishes. We conducted separate trials with each of the three foods with the following numbers of 5-cm dishes per box: 0, 1, 2, 4, 8, and 12. PROC MIXED in PC-SAS 9.0 (SAS Institute, Cary, NC) was used to determine whether the total number of eggs laid was affected by the number of available dishes. In trials with two to 12 dishes, we ranked dishes in descending order with respect to the number of eggs and calculated the average number of eggs laid for each ranking score.

Indices Used to Describe Distribution of Eggs. The variance/mean ratio has been suggested as both a measure of randomness and an index of aggregation (Southwood 1978, Sokal and Rohlf 1981), largely because variance/mean = 1 in the Poisson distribution and therefore departures from unity were thought to provide unique information about the observed distribution. However, Hurlbert (1990) showed that: 1) many very different distributions, including bimodal, skewed, and symmetrical, could have the same variance/mean ratio; and 2) it is unreasonable to expect a single index to express both departure from randomness and degree of aggregation. Instead, Hurlbert (1990) proposed an index corresponding to randomness, D_p, which is based directly on the degree of overlap between the observed and Poisson distributions. The D_p index varies between 0–1, and is directly related to the degree of overlap between the observed distribution and a Poisson (random) distribution with 0 being 100% concordance and values approaching 1 indicating increasingly non-Poisson distributions of eggs. The D_p index was calculated for each trial. Secondly, Hurlbert (1990) recommended that the Morisita index (Morisita 1959), I_m, or Lloyd index (Lloyd 1967) to be used as indices of aggregation. As a measure of aggregation for each trial, we calculated the Morisita index (Hurlbert 1990), I_{m2}. The I_{m2} index measures, for a pair of eggs randomly selected from all the eggs in the experiment, the degree to which the probability of finding both eggs in the same dish "is greater or less than it would be if individuals [eggs] were randomly distributed. It equals 1.0 for random distributions and for non-random distributions can assume values from 0 to $+\infty$" (Hurlbert 1990, p. 266). D_p indices were transformed as the arcsine of the square root, and I_{m2} indices were transformed as the natural logarithm in order to stabilize the variance and the residuals were visually inspected. Two-way ANOVA was conducted on the data (JMP statistical software, SAS Institute, Cary, NC) and Tukey HSD post hoc contrasts were conducted within the significant main effects.

Results

Number of Oviposition Events. From monitoring of *P. interpunctella* oviposition in 3-h intervals, we showed that *P. interpunctella* females laid eggs 6.40 ± 0.56 (mean ± SE, range 3–9) times during 48 h. The average total oviposition per *P. interpunctella* female during 48 h was 176.8 ± 29.3, and the highest number of eggs laid in a single 3-h interval was 232. In addition, we showed that there was a significant positive correlation between number of oviposition events and total oviposition for the 48-h time period (Fig. 1).

Ovipositional Response to Size of Dishes. In trials with one large and two small dishes, the relationship between observed and predicted numbers of eggs in the large dish was quite similar for the three foods (Fig. 2). For all three foods the linear regression analyses were highly significant ($P < 0.01$), and the number of eggs laid in the large dish was most similar (the slope was closest to 1) to what would be expected based upon the surface area of food compared with the predictions based upon number of dishes and/or volume of food. For all three foods, the slope of regression lines was <1, which means that *P. interpunctella* fe-

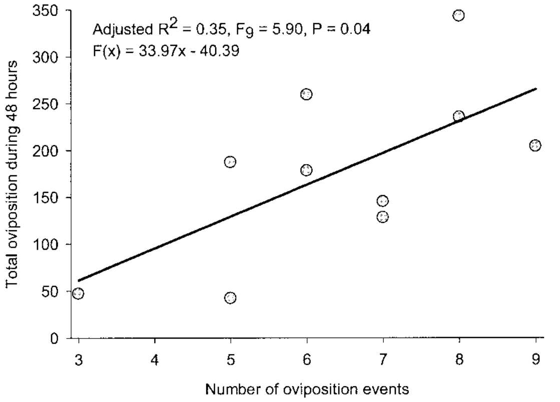

Fig. 1. Correlation between number of recorded oviposition events during 48 h and total oviposition by single *P. interpunctella* females.

males consistently laid fewer eggs than expected in the large dish.

Ovipositional Response to Resource Value of Dishes. When *P. interpunctella* females were given a choice between dishes of different resource value, the oviposition on cracked wheat at all dish densities was not significantly different ($P > 0.05$) from what would be expected if *P. interpunctella* females showed no preference. However, the number of eggs in the improved dish containing oil-treated wheat was significantly higher ($P < 0.05$) than the oviposition in control dishes at all dish densities (Fig. 3).

Ovipositional Response to Number of Dishes. Very few eggs (6.9 ± 1.9, range 0–48) were laid when no dishes were offered, whereas 50–100 eggs were laid per day when one to 12 dishes were offered (Fig. 4). Of the 225 trials with one to 12 dishes, *P. interpunctella* females, on average, laid 6.3% of the eggs on the box floor outside dishes. Generally, there was a negative relationship between eggs oviposited on the box floor and number of dishes per trial. Excluding trials without dishes, there was a significant difference in total oviposition among foods ($F_{2,167} = 3.16$; $P = 0.045$) but no significant difference in total oviposition among trials with different numbers of dishes ($F_{3,167} = 2.11$; $P = 0.101$). For characterization of the distribution of eggs among dishes, we ranked dishes in each trial and found that the difference in numbers of eggs between highest and lowest ranked dishes was generally high-

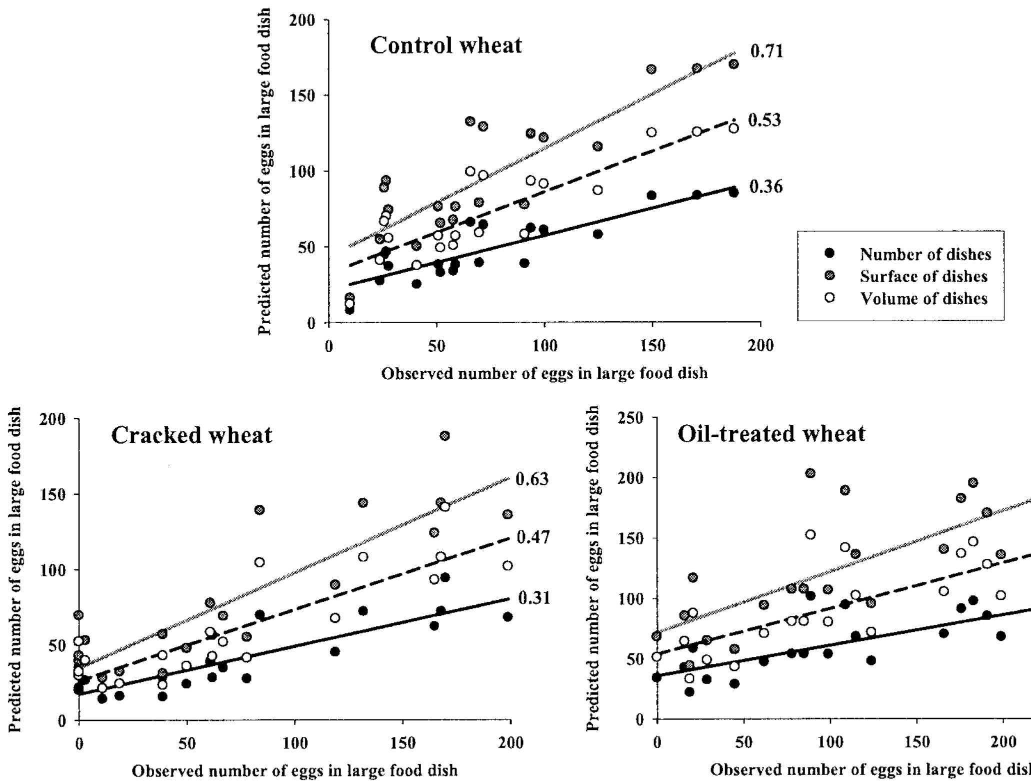

Fig. 2. Two 5-cm dishes containing 5 g of food and one 10-cm dish containing 10 g of food were used in all trials. Dots denote the expected number of eggs laid in the large dish according to three predictions of number of eggs in the large dish: 1) "Number" represents one-third of total oviposition assuming equal oviposition in all three dishes, 2) "Surface" represents 67% of total oviposition assuming oviposition in the three dishes according to their top surface area, and 3) "Volume" represents half of total oviposition assuming oviposition in the three dishes according to the volume of food. The slopes of regression lines are presented in bold.

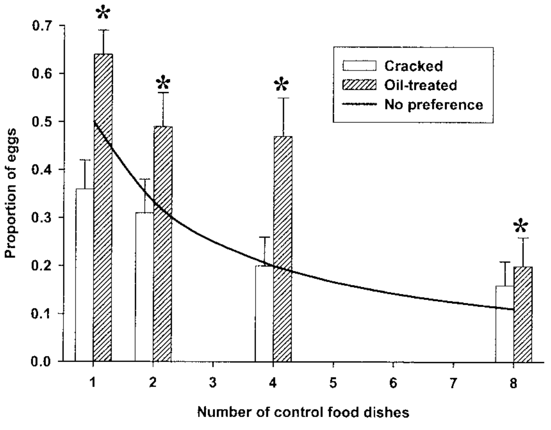

Fig. 3. Curve represents the expected proportion of eggs if *P. interpunctella* females laid as many eggs in the improved dish (cracked wheat or oil-treated wheat) as in control dishes, and bars represent the observed average proportion of eggs laid in the improved dish. *, significant difference between observed and expected ($P < 0.05$).

est for trials with oil-treated wheat kernels and lowest for those with control wheat kernels (Fig. 5).

Indices of Egg Distribution. D_p indices varied from 0.558 to 0.973 (Table 1), indicating that a Poisson distribution might not be a good model for egg distribution, and both food quality and number of dishes significantly affected this index (Table 2). The D_p index was significantly higher, indicating greater departure from a Poisson distribution, in the oil-treated wheat compared with the cracked or control wheat (Table 3). While D_p indices were significantly lower in trials with 12 dishes than in trials with 2, 4 or 8 dishes, the D_p values in general showed large differences between the observed and Poisson distributions. I_{m2} indices were significantly affected by both food quality and number of food dishes (Table 2). Oil-treated grain was associated with a significantly more aggregated distribution of eggs than either the control or cracked grain; two randomly-selected eggs in the oil-treated grain were, on average, about 86% more likely to come from the same dish than would be expected for randomly-distributed eggs. Likewise, moths presented with many oviposition sites (numbers of dishes) tended to lay their eggs in a much more aggregated fashion than moths presented with low numbers of dishes.

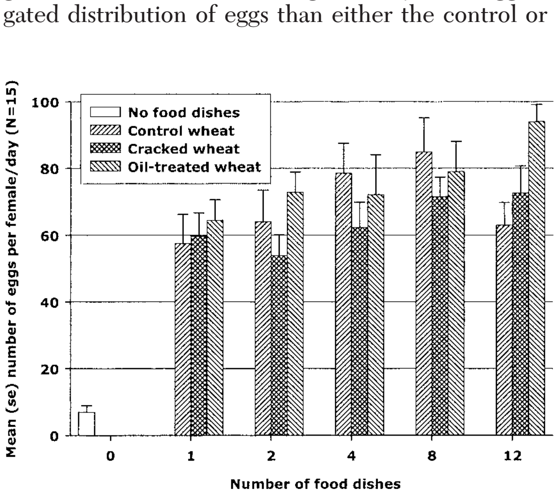

Fig. 4. Average total oviposition (eggs in dishes and on the box floor combined) in trials with different numbers of dishes and different foods.

Discussion

The experiments in this study were conducted in fairly small boxes in which only a single pair of young *P. interpunctella* adults was present in each trial. Therefore, important factors such as spatial scale and inter- and intraspecific competition were not accounted for, and time required for searching for oviposition sites was negligible. Such simplifications obviously restrict the extent to which these results can be used to describe the ovipositional strategy of *P. interpunctella* under field conditions. Despite these restrictions, the following was concluded from this study. 1) On average, *P. interpunctella* females laid eggs 6.4 times during 48 h. 2) *P. interpunctella* females laid consistently fewer eggs in large dishes than would be predicted from either number of dishes, surface area of dishes, and food amount in dishes. 3) In trials with cracked or oil-treated wheat kernels, the total oviposition was positively associated with the number of dishes, whereas no effect on total oviposition was observed with varying number of control dishes (plain untreated wheat kernels). 4) In trials with one dish containing improved food and others containing plain wheat kernels, *P. interpunctella* females preferred oil-treated wheat kernels, whereas they showed no preference for cracked or whole wheat kernels. 5) Using indices of randomness (D_p index) and aggregation (I_{m2} index), we demonstrated that the distribution of eggs was significantly different from a Poisson distribution, that it, was nonrandom, at all dish densities and for all the foods, that the distribution of eggs became increasingly aggregated with higher number of dishes and that this trend was most pronounced in trials with food with improved resource value.

Ovipositional Response to a Variety of Food Sources. Laboratory experiments have been used to describe ovipositional responses to both food quality and number of oviposition sites for several important stored-product insects, including rice weevil, *Sitophilus oryzae* (L.) (Coleoptera: Curculionidae) (Campbell 2002); red flour beetle, *Tribolium castaneum* (Herbst) (Coleoptera: Tenebrionidae) (Campbell and Runnion 2003); and *P. interpunctella* (Nansen and Phillips 2003). Nansen and Phillips (2003) conducted choice experiments with *P. interpunctella* adults and demonstrated that females laid significantly 1) fewer eggs when the food sources were screened compared with the same experiments with unscreened food sources in which females could contact the substrate; 2) more eggs on oil-treated wheat kernels in unscreened dishes compared with untreated wheat kernels; 3) more eggs on wheat kernels treated with

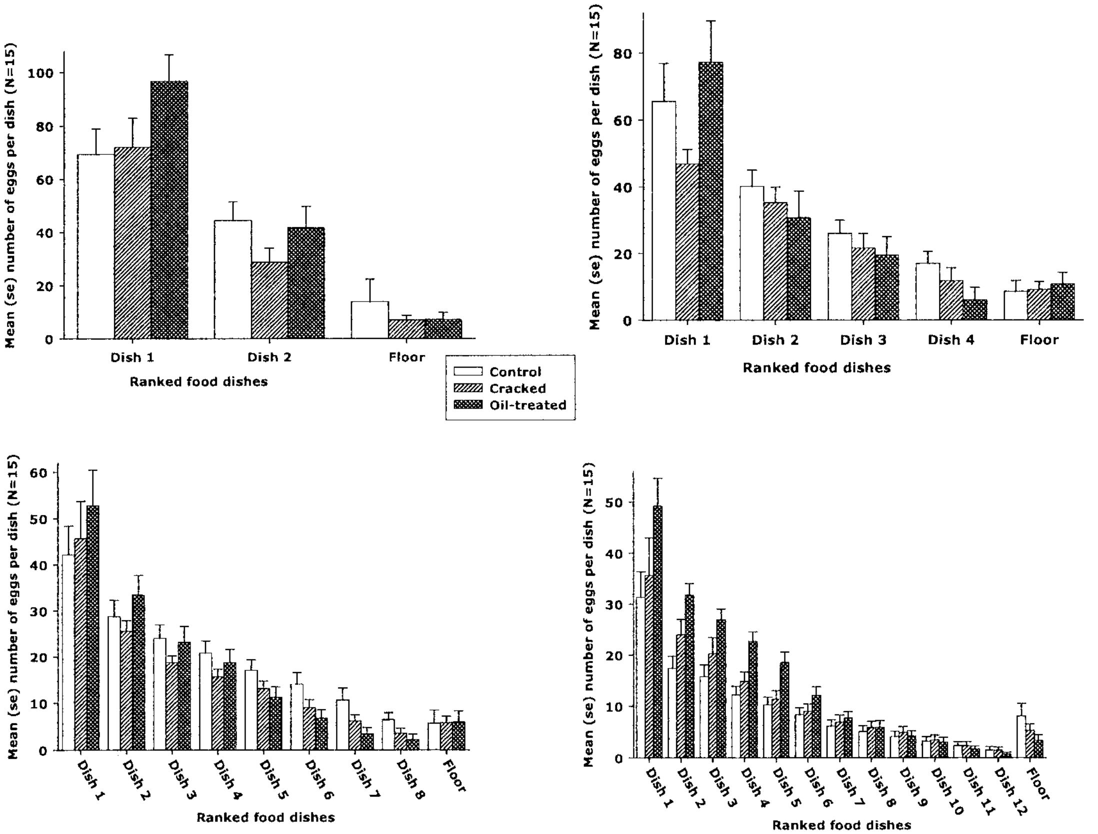

Fig. 5. For each combination of food and dishes, dishes were ranked in descending order according to number of eggs laid, and the average for each rank score was determined.

walnut oil compared with wheat kernels treated with one of 17 other oils; and 4) more eggs in dishes with wheat kernels treated with walnut oil in a nine-choice experiment also involving wheat kernels treated with seven other oils and untreated wheat kernels. Although the results by Nansen and Phillips (2003) indicated that *P. interpunctella* females responded to the resource quality of dishes, it was not known whether the distribution of eggs among dishes would be affected by the number of available dishes, and/or to what extent the distribution of eggs was relative to the resource value of dishes. In this study, we demonstrated that both in terms of total oviposition and distribution of eggs among available dishes, ovipositing *P. interpunctella* females responded differently to the three foods, and the preference for oil-treated wheat was most pronounced. Lecato (1976)

Table 1. Descriptive statistics of the D_p and I_{m2} indices

Food quality	No. dishes	No. reps	Avg (se) D_p index	Avg (se) I_{m2} index
Control	2	15	0.948 (0.014)	1.080 (0.032)
	4	14	0.904 (0.019)	1.373 (0.121)
	8	15	0.673 (0.052)	1.327 (0.087)
	12	14	0.558 (0.070)	2.367 (0.700)
Cracked	2	16	0.957 (0.012)	1.236 (0.082)
	4	16	0.903 (0.019)	1.536 (0.198)
	8	16	0.723 (0.039)	1.695 (0.219)
	12	15	0.572 (0.056)	1.872 (0.218)
Oil-treated	2	15	0.973 (0.011)	1.281 (0.100)
	4	15	0.923 (0.037)	2.232 (0.252)
	8	14	0.797 (0.041)	1.975 (0.303)
	12	14	0.778 (0.051)	1.965 (0.154)

The D_p index varies between 0–1, and is directly related to the degree of overlap between the observed distribution and a Poisson (random) distribution with 0 being 100% concordance and values approaching 1 indicating increasingly non-random distributions of eggs. Numbers in brackets are average D_p indices. The I_{m2} index (Hurlbert 1990) measures, for a pair of eggs randomly selected from all the eggs in the experiment, the degree to which the probability of finding both eggs in the same dish is greater than would be expected if eggs were randomly distributed. It equals 1.0 for random distributions and for non-random distributions can assume values from 0 to $+\infty$.

Table 2. ANOVA for the D_p and I_{m2} indices of food quality and number of dishes

Treatment	D_p index		I_{m2} index	
	F ratio	Prob.	F ratio	Prob.
Food quality	8.58	<0.001	6.57	0.002
Dish number	54.76	<0.001	11.73	<0.001
Food quality × dish number	0.87	0.518	1.30	0.262

For description of D_p and I_{m2} indices, see legend to Table 1. Two-way ANOVA was used to examine the effect of food quality and number of dishes on the two indices.

Table 3. Tukey HSD of back-transformed least squares means for the D_p and I_{m2} indices of food quality and dish number

Treatment	No. Reps	Avg (s.e.) D_p index	Avg (s.e.) I_{m2} index
Food quality			
Control	58	0.772 (0.031)a	1.525 (0.180)a
Cracked	63	0.792 (0.026)a	1.580 (0.096)b
Oil-treated	58	0.870 (0.021)b	1.860 (0.115)c
No. dishes			
2 dishes	46	0.959 (0.007)a	1.200 (0.045)a
4 dishes	45	0.910 (0.015)a	1.717 (0.126)b
8 dishes	45	0.729 (0.026)b	1.660 (0.129)b
12 dishes	43	0.635 (0.037)b	2.064 (0.242)b

For description of D_p and I_{m2} indices, see legend to Table 1. Two-way ANOVA with Tukey HSD post hoc contrasts was conducted to examine the effect of food qualities and numbers of dishes. Different letters denote statistical difference ($P < 0.05$).

showed that *P. interpunctella* survival is higher on cracked grain than whole grain, but it is not known whether addition of walnut oil to whole grain increases the survival of *P. interpunctella* as well. Also, the walnut oil constituents that seem to be responsible for the positive ovipositional response by *P. interpunctella* females are not known, but preliminary analysis of the used walnut oil suggested that *P. interpunctella* females may be responding positively to free fatty acids (Nansen et al. 2003b). Zeleny (1954) and Demianyk and Sinha (1987) described how the respiration of damaged grain increases, leading to a subsequent increase in moisture content and enzymatic breakdown of lipids by fungi that ultimately causes an increase in free fatty acid content. Thus, to *P. interpunctella* females, a high content of volatile free fatty acids may be an indicator of deteriorated food that is more suitable for oviposition than control wheat.

Distribution of Eggs among Identical Dishes. Three trends in egg aggregation were observed: 1) in trials with 12 dishes, *P. interpunctella* females preferred, on average, to lay 25–30% of their total oviposition in one of the dishes for all three foods (Fig. 5); 2) in trials with more than four dishes, on average, 0.5–2.5 dishes contained no eggs; and 3) *P. interpunctella* females were generally more likely to "lay most of their eggs in one basket" in trials with improved foods than in those with plain wheat kernels (Fig. 5). On the basis of these studies, it seems reasonable to speculate that an oviposition bait with efficient long-range attractants and with highly improved resource value would elicit a strong ovipositional response by *P. interpunctella* females and thereby provide considerable protection of valuable food items. The results presented here suggest that further research is needed into the basic physiology and biochemistry associated with the selection of oviposition sites by stored product moths. In addition, it justifies further applied research of extraction of food-derived compounds (including food oil extracts) and how these can be used to lure ovipositing females into trapping devices or bait stations.

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